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Review of adult diapause in ichneumonid wasps (Hymenoptera, Ichneumonidae)

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Abstract
The mechanisms and ecological circumstances of adult diapause in Ichneumonidae are poorly studied. An overview is presented of what observations and research have been carried out on ichneumonid diapause to date, and new ecological and distributional data are presented. The new data primarily concerns species that hibernate in association with trees, based on observations made in Belgium and the Netherlands. A preliminary checklist of the 50 species that are now known to hibernate is provided for both these countries. *Auberteterus alternecoloratus* (Cushman, 1929), *Dicaelotus montanus* (de Stefani, 1885), *Dicaelotus pictus* (Schmiedeknecht, 1903) and *Orthocentrus sannio* Holmgren, 1858 are reported as adult hibernators for the first time. Four species are newly recorded for the Belgian or Dutch faunas.

Keywords
Darwin wasps, diapause, ecology, hibernation

Introduction

Diapause is a broad concept used to designate a dynamic process in several successive phases of low metabolic activity, at least partially genetically determined, with the neuro-hormonal system as mediator (Denlinger 2002; Kostál 2006). It serves to help face and survive seasonal changes (mostly in temperature and humidity) at a low energetic cost (Hahn and Denlinger 2007; Tougeron 2019). Diapause may occur at any stage of life: egg, larval, pupal or adult; the latter is also called reproductive

diapause (Denlinger 2002; Quicke 2015). During adult diapause, respiration rate declines and the reproductive functions are put on hold (Fielding 2008; Chen et al. 2012; Hodek 2012).

Depending on the seasonal characteristics, specific terminology is used such as summer diapause or aestivation and winter diapause or hibernation. The latter has generally received most attention (Tougeron 2019). It is important to note these terms do not correspond well to the timing of the seasons in the field: winter diapause may begin as early as midsummer for example (Hodek 2012). In obligate diapause, species arrest development regardless of environmental conditions, whereas in species with facultative diapause, external conditions do have an impact and determine whether the species undergoes diapause or not (Hahn and Denlinger 2007). Recent studies suggest both tendencies are highly flexible, experiencing phenotypic plasticity, and may thus be mixed at species or even population level, inherently resisting any kind of generalization (Hodek 2012; Tougeron et al. 2018a, b).

It is agreed that photoperiodism, the physiological reaction of organisms to day length, is the key factor in regulating adult diapause (Hodek 2012; Tougeron 2019). Consequently, a different geographic latitude possibly results in differing diapause strategies, caused by the specific photoperiodic regulation at population level (Hodek 2012). A second crucial aspect seems to be temperature. Several studies suggest how, next to photoperiodism, temperature plays an important role in regulating adult diapause (Sgolastra et al. 2010; Chen et al. 2012), even in areas with a similar latitude (Tougeron et al. 2018a). On a biochemical level, it is known how glycerol levels, which contribute significantly to maintain metabolism and the utilization of metabolic reserves (Storey and Storey 1990; Denlinger 2002), will increase through a specific phosphorylation mechanism, starting from 0–5 °C (Hahn and Denlinger 2007). Furthermore, respiration rates decrease at lower temperatures. In general, energetic costs are reduced in that case (Hahn and Denlinger 2007). Other possible factors governing diapause are food availability and quality, humidity and population density (Hodek 2012).

While adult diapause is very common in some orders, especially Coleoptera and Hemiptera (Heteroptera), the incidence of this phenomenon is far lower among the Lepidoptera and Hymenoptera, involving approximately 5% of the temperate species in each (Hodek 2012). In the Ichneumonidae, although there has been some research on diapause (mainly) in early life phases (Claret 1973, 1978; Aeschlimann 1974; Griffiths 1975; Renfer 1975; Arthur and Mason 1985; Shaw and Wahl 1989; Coop and Croft 1990; Zijp and Blommers 2002a; Humble 2006), the majority of studies have focused on adult hibernation. Some studies on hibernating ichneumonids have contributed significantly to our more general understanding of diapause. For example, Duffield and Nordin (1970) demonstrated the relationship between presence or absence of glycerol synthesis and hibernation among North American species. Hibernating ichneumonids mainly belong to the subfamily Ichneumoninae, although a few examples from Cryptinae, Orthocentrinae, Metopiinae, Phygadeuontinae and Pimplinae are also known (Quicke 2015 and see Discussion). It is important to note this review principally addresses 'free living' adult wasps. More exceptionally species

pass much of the year as cocooned adults (e.g. several Campopleginae) or as cocooned pharate adults (e.g. Agriotypinae and some *Lissonota* spp.) (see Quicke 2015 and Shaw et al. 2016 for some examples).

The hibernating 'free living' adult wasps are always fertilized females, having mated before entering diapause. During hibernation the female's abdomen sometimes appears to be swollen, due to the ripening of the ovaria (Bischoff 1927; Leruth 1939; Selfa and Escola 1991). When diapause reaches its end the females are ready to start searching for hosts. Tereshkin (1996) suggests how adult hibernators benefit from using specific mechanisms for coping with harsh(er) climatic conditions although these have been little studied. Further, little attention has been given to phenological synchronicity between adult (hibernating) parasitoid wasps and their hosts, an interesting and unique relationship, which could be destabilized by climate change (Godfray 1994; Tougeron et al. 2021).

To date, most studies have been on hibernating species themselves and their different diapause sites or hibernacula, which are known to affect diapause energetics and costs by, for example, decreasing metabolic rates (Hahn and Denlinger 2007). These sites are useful to structure observations because species tend to be site-specific, meaning they specialize in a specific ecological niche to hibernate. Examples are (old) buildings, caves, under stones or moss, among grass tussocks or even near the top soil layer between dense conifer foliage (e.g. pine needles) or leaf litter. Trees, both living and dead, are also used as hibernation sites.

Even within this range of hibernacula types, it is important to consider all conditions, as there can be small but important differences that may influence abundance and usage. For example, hibernating ichneumonids are possibly more common in caves with higher temperatures (Novak et al. 2010). Publications on hibernating ichneumonid wasps unfortunately do not always specify the hibernacula, and often implicitly focus on tree hibernation. Important works for the Palaearctic are summarised by country in Table 1. In addition, there are a number of unpublished observations we are aware of, and many other publications in which hibernation is mentioned only as a side note (see Verheyde 2022, in prep.). Studies related to particular types of hibernacula are discussed below and listed in Table 2. The total number of ichneumonid species that have been reported to hibernate is unknown but is at least 393 species worldwide (Yu et al. 2012).

Table 1. Major compilatory works on ichneumonid hibernation by country.

Country	References
Austria	Hinz and Kreissl (1992, 1993)
Belarus	Tereshkin (2002, 2004, 2011)
France	Berthoumieu (1894a, 1894b, 1895a, 1895b, 1896), Seyrig (1923)
Eire (Ireland)	Johnson (1912, 1920)
Germany	Tischbein (1871), Heinrich (1951), Bauer (1961), Sebald et al. (2000, 2001)
Romania	Constantineanu (1929a, 1929b; 1959; 1965)
Russia	Rasnitsyn (1964)
United Kingdom	Morley (1903)

Table 2. Past research on particular hibernaculum type and country.

Hibernaculum type	Country	References
C	Czech Republic	Sedivy and Dvorak (2002)
C	Hungary	Vas and Kutasi (2016)
C	Luxemburg	Sebald and Weber (2013)
C	Portugal	Penado et al. (2013)
C	Serbia	Zikic et al. (2020)
C	Slovenia	Novak et al. (2010)
C	Spain	Selfa and Escola (1991)
C	United Kingdom (Scotland)	Baird and Shaw (2019)
T	Bulgaria	Kolarov (1992)
T	France	Pic (1917, 1919), Valemberg et al. (1974a, 1974b, 1975a, 1975b, 1976a, 1976b, 1978, 1979, 1982, 2013), Pénigot (2020)
T	Germany	Hilpert 1987; Sebald et al. 2001
T	North America	Townes (1938), Dasch (1971), Smith (1932: one case)
T	Romania	Constantineanu (1969, 1970), Lungu-Constantineanu and Constantineanu (2014)
T	Russia	Rasnitsyn (1959)
T	The Netherlands	Van Dinther (1951: one case)

Materials and methods

Additional to existing literature, two datasets were used. The first dataset consists of the data exclusively gathered by the first author, specifically by searching for ichneumonid wasps on dead wood. To have an overview of his own field excursions, a fixed template in Microsoft Excel was used. So far, 53 excursions were entered, dating from 3 November 2018 to 20 February 2021 with a total searching time of 72.5 hours. Each excursion lasted for at least 30 minutes, and at least 10 trees had to be available to check. Subsequent variables were noted: location, date, temperature, daytime, searching time, amount of people searching, trees checked (approximation margin of 5), dominant tree species (> 5 present), other tree species, numbers of individual wasps found, amount of species found. Approximately 1515 tree trunks were checked and the average temperature was 9 °C. On average, it took three trees and 8 minutes and 30 secs to find a hibernating wasp. In one area, on average, 10 individuals of 3 different species were found. In order to limit ecological impact, the same area was never investigated twice in one season.

The second dataset consists of validated data entered in the citizen science portals *waarnemingen.be* and *waarneming.nl*. For the first author's own observations, which were also entered, extra information was noted down at the level of individuals: species found together, tree species, tree diameter and any other interesting information (dead specimens, the position of the tree, etc.). Coordinates and exact timestamps were automatically linked when adding the findings via mobile phone. The second dataset also contains (live) data from other observers on *waarnemingen.be* and *waarneming.nl*. All data has been validated by the author and is freely available on the portals and partially on GBIF (https://doi.org/10.15468/r0fx1v). The set was harvested and analysed manually for all data entered before 1/10/2021. Both datasets will be used and

merged more profoundly in a future study, and published with open access, which is why this study is preliminary. Specific observations from the portals are referred to with a unique identifier, called the ObsID (= unique identifier on GBIF); which can be placed in the browser to search for; for example https://waarnemingen.be/waarneming/view/169516420 or https://waarneming.nl/waarneming/view/226649126

Combining both datasets, in total 1120 records involving a total of 50 different species, were included in this study. A record is defined as a finding at one specific locality at one moment in time, unrelated to individual numbers at that locality (see also Table 3). Moreover, a record was deemed valid when a) the species could be safely identified to species (or species-complex) and b) it could be seen as hibernating. Hibernation was mainly defined by the presence of the wasp in a hibernaculum and/or exceptionally other contextual aspects such as temperature and phenology (see also Discussion). In cases of doubt we did not include the record. At the level of individual specimens, 524 wasps of 16 species were found by the first author.

Results

Caves

Besides the general studies mentioned above, specific studies of ichneumonids hibernating in caves are shown in Table 2 (C) and our results are given in Table 3 (C). From these it is apparent that a number of genera within Ichneumoninae are highly associated with this type of hibernaculum, specifically *Amblyteles armatorius* (Forster, 1771), *Diphyus* spp. and *Exephanes* spp. Structural observations made in Belgium and the Netherlands are mainly situated in two regions: the calcareous and hilly slopes in certain parts of Wallonia and the limestone quarries near Maastricht (the Netherlands). More casually, some species have also been found hibernating in bunkers or within old city walls (B; Table 3), often observed by people searching for bats (Verheyde 2020). Of these, the most common were *Diphyus quadripunctorius* (Müller, 1776) and *Exephanes ischioxanthus* (Gravenhorst, 1829). Our data show that hibernating *D. quadripunctorius* form aggregations, sometimes reaching huge numbers, while for *E. ischioxanthus* only a few specimens at most are found in any given place. For example, in one local cave complex, 624 specimens of *D. quadripunctorius* were counted (ObsID: 182944573; Fig. 1). Rare reports of other species found hibernating are *Diphyus castanopyga* (Stephens, 1835), *Diphyus palliatorius* (Gravenhorst, 1829) and *Exephanes riesei* (Habermehl, 1916). Lastly, there is also *Amblyteles armatorius*. A sole observation (ObsID: 169516420) on 9 September 2018 of twenty females hibernating in the crypt of the church of Saint-Hubert (Liège, Belgium) confirm a possible summer diapause of this species, as suggested by Hinz (1985) and Burmeister and Diller (1997). Both aestivating and overwintering specimens of *A. armatorius* and *D. quadripunctorius* have been observed (Ginet and Decou 1977), but to date there are no certain records of consistent diapause for Belgium and the Netherlands. Those species that specialise in (artificial) caves, mines or buildings (B, C; Table 3) are only rarely found hibernating in any other diapause sites.

Figure 1. Females of *Diphyus quadripunctorius* (Müller, 1776) hibernating in a limestone cave in the Netherlands, Maastricht (Sint-Pietersberg), 4 December 2019. Willem Vergoossen.

Vegetation and litter

While cave complexes have been somewhat systematically searched for hibernating wasps, the zone near the soil (under stones, pine needles, in litter, in vegetation) has very seldom been searched, including for Belgium and the Netherlands. The observations that we have were mostly made incidentally.

In the United Kingdom especially, 'tussocking' (Pearce 1948) has a great tradition among entomologists, and many species can be found hibernating in grass tussocks (Morley 1903; Hancock 1923, 1925; Perkins 1959; M. Storey, pers. comm.; LV in Table 3). There is no doubt that more species specialize in this hibernaculum type than any other. When we take a look at species composition, species often belong to the tribe Phaeogenini (subfamily Ichneumoninae) or the subfamily Phygadeuontinae and tend to be remarkably smaller (Pénigot 2020; see also Discussion). Indeed, our only finding of the phaeogenine wasp *Auberteterus alternecoloratus* (Cushman, 1929) was in a stem of *Heracleum sphondylium* L. (ObsID: 209784725). Six specimens of *Ichneumon inquinatus* (Wesmael, 1845) were found in the stems of *Carex paniculata* L.; a rare example of crossing-over niches as this species is also often found hibernating under bark (see below; ObsID: 206576096). Finally, one specimen of *Ichneumon sarcitorius* Linnaeus, 1758 was found under a rosette of *Verbascum nigrum* L. (ObsID: 186199416). Slightly more successful was searching in or under decaying leaves, conifer needles or grass, sometimes related to

Figure 2. A female of *Diphyus amatorius* (Müller, 1776), found hibernating beneath decaying leaves, while searching for heteropterans; the Netherlands, Ommen (Varsenerveld), 13 November 2019. Gerard Beersma.

compost bins (DV; Table 3): *Centeterus confector* (Gravenhorst, 1829), *Colpognathus celerator* (Gravenhorst, 1807), *Diadromus collaris* (Gravenhorst, 1829), *Diphyus amatorius* (Müller, 1776) (see Fig. 2), *Herpestomus brunnicornis* (Gravenhorst, 1829), *Ichneumon xanthorius* Förster, 1771 and *Spilothyrateles illuminatorius* (Gravenhorst, 1820) belong to this category.

Trees

Most studies on hibernating ichneumonids involve use of trees as hibernacula, either living trees or more often dead ones. Past research is summarised in Table 2 (T). For living trees (LT; Table 3), species have been found sheltering underneath removable bark. *Dicaelotus pictus* (Schmiedeknecht, 1903) and *Heterischnus truncator* (Fabricius, 1798) were both found on living *Platanus* spp., the latter also known as a hibernator on dead wood (DT; Table 3). Individuals have also been reported hiding in cracks of the bark of living trees, sometimes covered with moss (Lungu-Constantineanu and Constantineanu 2014), but no such observations have so far been made in the Low Countries. More exceptionally, evergreen trees or plants such as ivy (*Hedera*) may be used as shelter, as ladybugs (Coleoptera: Coccinellidae) sometimes do. For example, conifers in the case of *Itoplectis maculator* (Fabricius, 1775) (Pimplinae) (see Fig. 3),

Table 3. Preliminary checklist of species hibernating as adults in Belgium and the Netherlands with number of unique records (author results in parenthesis). Record = finding at one specific locality at one moment in time, unrelated to individual numbers at that locality* = Reported as adult hibernator for the first timeColl. = Hibernating species in collection of the author or someone else*Hibernacula = B: Building – C: Cave – DT: Dead tree – DTCL: Dead tree clay – DV: Decaying vegetation – LV: Living (standing) vegetation - LT: Living tree – O: Other (mentioned in text) – S: Stone.

Subfamily, tribe, species	Country		Hibernacula	Coll
	BE	NL		
ICHNEUMONINAE				
ICHNEUMONINI				
Amblyteles armatorius (Forster, 1771)	1	3	B, C	
Aoplus defraudator (Wesmael, 1845)		1	DT	
Barichneumon peregrinator (Linnaeus, 1758) [Dinther 1951]		1	DT	x*
Chasmias motatorius (Fabricius, 1775)	5 (1)	8	DT	x
Chasmias paludator (Desvignes, 1864)	7 (2)	5	DT	x
Diphyus amatorius (Müller, 1776)		1	DV	
Diphyus castanopyga (Stephens, 1835)		1	C	x
Diphyus palliatorius (Gravenhorst, 1829)		1	C	x
Diphyus quadripunctorius (Müller, 1776)	53	95	B, C	x
Diphyus restitutor (Wesmael, 1859)		2	B, DT	
Exephanes ischioxanthus (Gravenhorst, 1829)		7	C	x
Exephanes riesei (Habermehl, 1916)		2	C	x
Hoplismenus bidentatus (Gmelin, 1790)	2		DT	x
Hoplismenus bidentatus/bispinatorius (Thunberg, 1824)	16 (1)	26	DT, O	
Hoplismenus terrificus Wesmael, 1848	1	3	DT	
Ichneumon albiger Wesmael, 1845	6 (3)		DT	x
Ichneumon bucculentus Wesmael, 1845	56 (24)	12	DT, DTCL	x
Ichneumon confusor (Gravenhorst, 1820)	2		DT	x
Ichneumon crassifemur Thomson, 1886	2		DT	
Ichneumon extensorius Linnaeus, 1758	1 (1)	1	DT	x
Ichneumon gracilentus Wesmael, 1845	6 (1)		DT	x
Ichneumon inquinatus (Wesmael, 1845)	34 (16)	7	DT, LV	x
Ichneumon lugens Gravenhorst, 1829	88 (28)	53	DT, O	x
Ichneumon luteipes Wesmael, 1855	1		DT	
Ichneumon melanotis Holmgren, 1864	3 (3)		DT	x
Ichneumon primatorius Forster, 1771	1	2	DT	
Ichneumon sarcitorius Linnaeus, 1758		2	S, LV	
Ichneumon stramentarius Gravenhorst, 1820	1		DT	x
Ichneumon stramentor Rasnitsyn, 1981	112 (51)	74	DT	x
Ichneumon suspiciosus Wesmael, 1845	61 (55)	3	DT, O	x
Ichneumon xanthorius Forster, 1771	2	3	S, DV	
Ichneumon stramentarius/suspiciosus	10	6	DT	
Ichneumon albiger/extensorius/gracilentus	11	11	DT	
Lymantrichneumon disparis (Poda, 1761)	81 (28)	25	C, DT, DTCL	x
Spilothyrateles illuminatorius (Gravenhorst, 1820)		3	DV	
Stenichneumon culpator (Schrank, 1802)	155 (64)	56	DT, DTCL	x
Stenichneumon militarius (Thunberg, 1824)	3 (1)		DT	x
Syspasis albiguttata (Gravenhorst, 1820)	1	1	DT	
Syspasis scutellator (Gravenhorst, 1829)		1	DT	
Zanthojoppa lutea (Gravenhorst, 1829) nov. sp. NL	20 (4)	2	DT	x

Subfamily, tribe, species	Country		Hibernacula	Coll
	BE	NL		
PHAEOGENINI				
Auberteterus alternecoloratus (Cushman, 1929)* nov. sp. BE	1		LV	x*
Centeterus confector (Gravenhorst, 1829)	1	1	LT, DV	x*
Colpognathus celerator (Gravenhorst, 1807)		1	DV	
Diadromus collaris (Gravenhorst, 1829)		1	DV	
Dicaelotus montanus (de Stefani, 1885)* nov. sp. BE	1		LT	x*
Dicaelotus pictus (Schmiedeknecht, 1903)* nov. sp. BE	1		LT	x
Herpestomus brunnicornis (Gravenhorst, 1829)		1	DV	x*
Heterischnus truncator (Fabricius, 1798)	4	2	DT, LT, O	
ORTHOCENTRINAE				
Orthocentrus sannio Holmgren, 1858*	1		DT	x
CRYPTINAE				
Agrothereutes abbreviatus (Fabricius, 1794) (?) cf. text		1	DT	
PIMPLINAE				
Itoplectis maculator (Fabricius, 1775)	1	1	LT	
Pimpla turionellae (Linnaeus, 1758)		1	DT	
Scambus pomorum (Ratzeburg, 1848) [Zijp and Blommers 2002b]		1	LT	

Scambus pomorum (Ratzeburg, 1848) (Pimplinae) and, reported here as a hibernator for the first time, *Dicaelotus montanus* (de Stefani, 1885) (Hancock 1925; Cole 1967; Zijp and Blommers 2002b). These species can be found by 'beating' the vegetation or for example branches of a tree.

Dead wood was examined extensively by the first author. Although the present results are only preliminary, they suggest the highest quantities of ichneumonid wasps are to be found on fallen, large diameter dead trees, although this is not a strict requirement (see also Valemberg 1974a). The state of the decaying tree is important (Townes 1938; Rasnitsyn 1959; Bauer 1984; Sebald et al. 2001). When the tree fell only recently, the bark cannot be infiltrated. When the tree is completely rotten, humidity is too high, and too many fungi or other organisms are present. Ichneumonid wasps were seldomly found on trees infected by fungi like *Armillaria* (Fr.) Staude spp. on *Populus* L. spp. (see Fig. 4) or *Coprinellus* spp. P. Karst, probably because the fungi create air currents beneath the bark and alter the conditions there. Infrequently specimens were found in decayed wood with no more bark left, but this mostly happened on concealed and 'clean' pieces of rather wet wood. When there is bark, it is best removed at an angle of +- 45 degrees.

Despite being mentioned in the literature, moss on tree bark was only very seldom used as shelter itself (see also Pic 1917; Rasnitsyn 1959; Pénigot 2020). In doubtful cases the ichneumonid wasp was usually attached to strongly decayed bark at the lower side of the moss couches. In most cases the moss mostly appeared to be nothing more than a by-product demonstrating the age of the decaying tree. We agree with Sebald et al. (2001) that moss could have an important function in regulating temperature and humidity, but in contrast to their conclusions and those of, for example, Valemberg in France (e.g. Valemberg 1974a) we could not observe any preference in

Figure 3. A female of *Itoplectis maculator* (Fabricius, 1775) found in hibernation position on *Pinus sylvestris* L. in the Netherlands, Eindhoven (Stratumse Heide), 12 November 2020. Ruut Aussems.

Figure 4. A rare example of a hibernating ichneumonid wasp, *Ichneumon bucculentus* Wesmael 1845, near hyphae of an *Armillaria* (Fr.) Staude sp.; Belgium, Moerbeke (Bosberg), 13 January 2021. Patrick Debeuf.

Figures 5. Example in Belgium of trees used by several ichneumonid wasps to hibernate beneath the bark; *Quercus robur* L., Zillebeke (Hogebos), 14 February 2020 and *Pinus sylvestris* L., Zillebeke (Papenelst), 23 December 2019. Fons Verheyde.

relation to hibernacula from the wasp's perspective. Possibly, the role moss plays is more important for another hibernation type, namely the clay or mud between the tree roots (see also Discussion), but in order to make any conclusions on this topic we need more data.

Some tree species appear to be more suitable for hibernating ichneumonids than others, depending on the bark material (thickness, structure) and again the level of moisture or humidity. Most species have been found associated with *Quercus* L. and *Populus* L. spp., while for example *Fagus* L. spp. and conifers were less used as hibernacula (see also Tereshkin 2002 and Figs 5–6.). Both *Quercus* and *Populus* produce good quantities of bark humus (see Figs 7–8), where wasps like to hibernate, likely enjoying more stable climatic conditions. Species hibernating on dead wood in the Low Countries are rather large (> 12 mm) Ichneumoninae, placed in the genera *Hoplismenus*, *Ichneumon*, *Lymantrichneumon* and *Stenichneumon*. Less common are *Chasmias* spp. Some genera are rare, for example *Aoplus* and *Syspasis* spp. *Orthocentrus sannio* (Orthocentrinae) and *Pimpla turionellae* (Pimplinae) constitute the only certain observations of hibernating species on dead trees not belonging to the subfamily Ichneumoninae.

There are some species-specific habits that have previously not been reported. For example, *Stenichneumon culpator* (Schrank, 1802) is nearly always found as solitary individuals, very often dug in beneath the bark, using 'spots' or insect galleries from

Figures 6. Example in Belgium of trees used by several ichneumonid wasps to hibernate beneath the bark; *Quercus robur* L., Zillebeke (Hogebos), 14 February 2020 and *Pinus sylvestris* L., Zillebeke (Papenelst), 23 December 2019. Fons Verheyde.

beetles or other xylophagous insects (Fig. 7; Valemberg 1974b). *Ichneumon* spp. characteristically form hibernation aggregations, often as a mix of different species and genera (Fig. 8; Seyrig 1924; Sebald et al. 2000; Valemberg 2013). Highest densities found involved *Ichneumon inquinatus* (Wesmael, 1845), with 17 specimens at one spot. *Hoplismenus* spp., which tend to avoid other species (confirming Constantineanu 1929a), were found more often on standing dead wood.

No signs of predation were found, even though wasps were found next to hibernating carabid beetles (Fig. 7). Of 524 specimens only two dead specimens were found: one specimen of *Lymantrichneumon disparis* (Poda, 1761) with traces of fungus (Fig. 9) and one specimen of *Stenichneumon culpator* (Schrank, 1802). The low mortality of hibernating Ichneumonidae on dead wood was previously mentioned by Rasnitsyn (1959) and Valemberg (2013). It can be generalised to other hibernacula as well (Baird and Shaw 2019).

Other

Some other hibernacula are only used occasionally (O; Table 3). For example, one hibernating individual of *Ichneumon suspiciosus* Wesmael, 1845 was found inside the shell of a chestnut (ObsID: 181301272; Fig. 10), a specimen of *Ichneumon lugens*

Figure 7. Female *Stenichneumon culpator* (Schrank, 1802), the most abundant hibernating ichneumonid wasp in the Low Countries, often hibernates in spots or galleries made by beetles (left). Here it is in hibernation next to *Carabus violaceus* Linnaeus, 1758; Belgium, Westouter (Rodeberg), 24 January 2022. Patrick Debeuf.

Gravenhorst, 1829 was discovered in a rotten tinder fungus (ObsID: 206166602); a specimen of *Heterischnus truncator* (Fabricius, 1798) was found hibernating between cardboard plates (ObsID: 167049565) and finally one specimen of the complex with *Hoplismenus bidentatus* (Gmelin, 1790) and *H. bispinatorius* (Thunberg, 1824) was found hibernating in a bird feeding house (ObsID: 182795650).

All results are listed in Table 3.

Discussion and future research

Related to our results, especially those concerning tree hibernation, several ecological questions will be investigated and hopefully answered in the future. Rasnitsyn (1959) and Valemberg (1974a) investigated the presence of ichneumonid wasps in respect to the orientation of dead wood, stating the northern (and eastern) side of the tree is more often used because it has more stable temperature and humidity, especially in regions where temperatures are more extreme. Similarly, it is likely that species specializing in dead wood prefer trunks deeper in the forest, where the sun seldom raises substrate temperatures (Dasch 1971). Modern technology will allow easy measurement of these ecological parameters.

Figure 8. Impression of several *Ichneumon* spp. hibernating in a thick layer of bark humus, in this case *Fagus sylvatica* L. with a diameter of 80 cm; Belgium, Torhout (Bos van Wijnendale), 28 December 2021. Patrick Debeuf.

Some authors, for example Sebald et al. (2001) and Tereshkin (2002) have commented on habitat types and that the suitability of wood may depend on whether it is standing or lying flat but both questions have not yet been explored fully. The hibernaculum used may not be fixed for the whole winter. When disturbed, wasps may move. Some have been observed to move further down the tree and shelter under undamaged bark, while others have fallen to the ground and dug themselves into the litter where they would not hibernate normally. It is possible that some more accessible types of hibernacula, for example the clay and mud between the roots of a fallen tree (DTCL; Table 3), provide space for 'temporary refugees' or species that need an escape route separate from their ideal or permanent hibernaculum and might explain some rare examples of species crossing over 'hibernation' niches.

Another question relates to body size. It is obvious that ichneumonids hibernating on wood (often Ichneumonini) are much larger on average (12–18 mm) in comparison to ichneumonid wasps hibernating in, for example, grass tussocks (often Phaeogenini; 6–10 mm; see also Pénigot 2020). As Pénigot states, the most plausible factor at play here seems to be cost efficiency and avoidance of energy loss. On average, smaller species have less fat reserves and are thus more sensitive to energy loss (Lease and Wolf 2011). Getting access to certain hibernacula such as dead wood can be more demanding than access to various other hibernacula such as decaying vegetation. Other physi-

Figure 9. A dead specimen of *Lymantrichneumon disparis* (Poda, 1761) with traces of unidentified fungi; Belgium, Zillebeke (Papenelst), 23 December 2019. Fons Verheyde.

ological barriers could also play a role, for example, limits of glycerol production or more generally the lack of antifreeze capability. On this subject more detailed research is crucial, for example to see if there are any differences among certain species or subfamilies (e.g. Shaw and Quicke 2000 on the braconid wasp *Acampsis alternipes* (Nees)). It is unclear how several surprisingly small ichneumonid wasps, such as *Orthocentrus* spp. (Orthocentrinae), often measuring around 5 mm, are able to hibernate in dead wood. Group clustering could be one part of the explanation (Rasnitsyn 1959 mentions up to 190 individuals in one case), but clearly does not suffice as many larger species use the same strategy (see above). The scarcity of findings suggests these species hibernate deeper inside the dead wood, several centimetres beneath the bark, rather than among the bark humus. Hypothetically then, they profit from thermal constancy deeper in the wood. It is unclear whether there is any difference in total overwintering time in comparison to larger ichneumonid wasps (presumably not). Further, it is not known why some larger ichneumonids, such as *Ichneumon sarcitorius* Linnaeus, 1758 and *Diphyus amatorius* (Müller, 1776), are only found in or under decaying vegetation and not on tree trunks. Perhaps biochemical analyses might provide insight.

A third aspect is the distribution and facultative nature of the diapause within some ichneumonid species. Some species are generally rare but can be locally abundant, and different local populations may show different diapause strategies. For example, *Ichneumon xanthorius* Forster, 1771 is extremely commonly observed in Belgium

Figure 10. A female of *Ichneumon suspiciosus* Wesmael, 1845, found hibernating in a chestnut shell buried and turned upside down in the ground; Belgium, Proven (Theetbos), 10 October 2019. Fons Verheyde.

and the Netherlands, with close to a thousand registered records every year, and is known to hibernate under stones (S; Table 1). However, this wasp has only been found hibernating in those countries a few times. The same can be said for many other species which are known to hibernate in other parts of the Western Palearctic (Verheyde 2022, in prep.), but are only caught during the flying season in Belgium and the Netherlands. This seems to suggest there are indeed intriguing differences at the population level, which were emphasized by, for example, Hodek (2012) and Tougeron et al. (2018b).

There is still much to learn about what life style features, such as nutritional ecology and oogenesis, may be shared by the taxa involved. Host-parasitoid relationships could be of particular importance because of the above-mentioned differences among populations or facultative nature of the diapause. For example, many *Ichneumon* spp. oviposit into host (pre-)pupae, whereas the other ichneumonine wasps mentioned in this paper attack late instar host larvae. The latter would allow slight koinobiosis to an extent, enabling some degree of nutrient absorption from host haemolymph by eggs that hibernating adults might have had limited capacity to yolk (Hinz and Horstmann 2007; M.R. Shaw, pers. comm.).

Finally, a critical analysis needs to be made of the past literature and checklists mentioned in the tables. This is in particular related to certain subfamilies, such as Cryptinae, Phygadeuontinae and to a lesser extent Pimplinae. For practical reasons, most researchers (including ourselves) implicitly accept a species as 'hibernating' when

it is found in a hibernaculum (for example, Rasnitsyn 1959: 'In addition, several species of Ichneumoninae [...] have been found in hibernation sites') and/or shows visual signs of diapause. However, the discovery of an adult ichneumonid wasp during the winter does not automatically mean that it is hibernating. For example, it could be active during the winter (possibly polyvoltine), it could be a species surviving in artificial conditions; optionally being connected to a host in urban structures (e.g. in a heated house), or it could be imported from another climate. For the Low Countries, there are several cases that could be classified as such. Even more troublesome is the presence of active wasps near natural hibernacula. In the Netherlands, the cryptine *Agrothereutes abbreviatus* (Fabricius, 1794), was found under bark on 16th December 2017 (ObsID: 146787701). Normally, this would be interpreted as hibernation, but it is possible the wasp was just actively searching for hosts there, instigated by changing climatic conditions. The same applies to (often apterous) females of several other cryptine and phygadeuontine genera and species, which have a long tradition of being accepted as adult hibernators (see for example Bischoff 1927). Careful examination is necessary case by case: some species, for example, do not hibernate as adults, some species hibernate as adults in the host cocoon and some hibernate as adults in litter (e.g. *Gelis proximus* (Förster 1850); Schwarz and Shaw 1999; Schwarz 2002). In the end, only molecular or biochemical analysis may provide a solution here.

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